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STUDIES IN THE HIPPOCASTANACEAE, III A HYBRID SWARM IN THE BUCKEYES

JAMES W. HARDIN

ONE particular population of shrubby buckeyes has caused a great deal of interest among taxonomists and naturalists for a number of years. This population of *Aesculus* is in Georgia, just northeast of Stone Mountain at the northeast edge of DeKalb County, on U. S. Route 78 (Atlanta to Athens). A large number of specimens, presumably from this population, are preserved in herbaria throughout the United States. One of the earliest of the collections was made in 1869 by Wm. M. Canby, one of the first botanists to visit this area after the Civil War (McVaugh, 1943). Later collections were made by J. K. Small (in 1891, 1893, 1895), C. S. Sargent (1899 and 1900), A. H. Curtiss (1901), T. G. Harbison (1911, 1912), W. W. Ashe (ca. 1920) and a number of more recent taxonomists. The Stone Mountain area is also of particular interest, in relation to buckeyes, since it is the type locality for *Aesculus georgiana* Sarg. and *A. georgiana* var. *pubescens* Sarg.¹ Also, the type of *A. harbisonii* Sarg. (*A. pavia* × *sylvatica*) was grown at the Arnold Arboretum from seed collected at Stone Mt. by Harbison in 1905.

I was first shown this population in the summer of 1952 by Wilbur H. Duncan who had made general observations on it for some time and who had become interested in the variation. There is no reason to think that this population has changed, significantly at least, since Canby and others visited there.

¹ In the original descriptions, Sargent (1913) cites a collection made by Harbison (No. 907, April 30, 1912) as the type for var. *pubescens*. There is no designation of the type for the species, however he did cite five specimens. Of these five syntypes, Sargent's collection dated April 16, 1900 is hereby designated as the lectotype for this species. Both type specimens are in the Arnold Arboretum Herbarium.

These early collections of Canby, Curtiss, Harbison, etc. show the same variation as the collections made by the writer in 1953.

The shrubs are two to seven feet tall and have a diameter of one half to two inches at the base. They form the dominant low shrub layer beneath a stand of mixed hardwoods and loblolly pine. The community is on the northeast-facing slope of one of the outlying ridges around Stone Mountain. This population of buckeyes covers an area of approximately one acre. The reason for the great attraction of the population is the striking and very apparent variation in a number of characters. The leaves are glabrous to densely tomentose, the shape and size of the inflorescence varies from short and broad to long and narrow, and the flower color particularly has an amazing array of combinations. One extreme in flower color is the red of both calyx and corolla. The other extreme is a pale yellow or often greenish-yellow in both calyx and corolla. Between these extremes one can find a flower to match nearly any shade and with the calyx usually more red than the corolla. The flowers on a single inflorescence are alike except for the variation in the color of the upper-petal claws which are yellow prior to anthesis and brown or orange after anthesis—regardless of general perianth color. Time of flowering also varies. During April when certain shrubs are in bloom, others right next to them are just beginning to blossom or leaf out and showing only the very small, crowded, green buds of the inflorescence.

Random samples of the population were collected on April 8, 1953 (Hardin No. 107). At that time nearly two-thirds of the shrubs in the population were in full bloom. Just over a month later (May 11th) another similar sample was collected (No. 129) at the same spot but from the shrubs then in bloom.

At the time of collection, speculations as to what this variation meant were based merely on general observations. There was no explanation for the variation in pubescence but it was of interest since both extremes were present and formed the basis for Sargent's designation of the two varieties. Also pubescence had been the basis for the distinction between *A. pavia* L. and *A. discolor* Pursh. The color variation was of particular interest since *A. pavia* of the Coastal Plain is typically red, and *A. sylvatica* Bartr. of the Piedmont is typically yellow.

Could this be a hybrid swarm between these two species? *Aesculus pavia* was certainly not found near here. The long flowering period certainly would include the typical flowering dates of these two species. But, the early-blooming shrubs were not predominately red-flowered. Of course this would not necessarily be expected.

Later, after closer examination of the pressed specimens, it was realized that another "key character" varied. This was the presence of stalked glands on the margin of the petals. *Aesculus pavia* typically has such glands; *A. sylvatica* is villous on the margins. Both conditions were found (but not necessarily with the corresponding perianth colors) and also an intermediate form with both hairs and glands on the margin. Thus it was impossible to identify to either species many of the specimens from this population.

In connection with a monographic study of *Aesculus* by the writer, these population samples have been analyzed using the techniques described by Anderson (1949). Each population sample consisted of 20–50 specimens. Every specimen was measured and scored for the following five characters: calyx length, stamen length, perianth color, pubescence of petal margin, and relationship of stamen length and lateral petal length (i.e., whether the length of the stamen is greater or less than that of the lateral petals). The first two characters are used as the coordinates of the graph, and the other characters are represented by symbols (Fig. 1). The data obtained from the analysis of the Stone Mountain population are presented graphically as pictorialized scatter diagrams in Fig. 1, graphs B and C.

A close examination of the behavior of individual characters in this population (as shown in the scatter diagrams) indicates influence from two directions. Using the method of extrapolated correlates (Anderson, l.c.), one can possibly extrapolate to the two hypothetical introgressants. Identification of these hypothetical species results in the names of *A. pavia* and *A. sylvatica*. As a check of the two suspected introgressing species, population analyses were made for *A. pavia* (Hardin No. 105 from Appling County, Georgia) and for *A. sylvatica* (No. 117 from Clarke County, Georgia). Results of the analyses of these populations

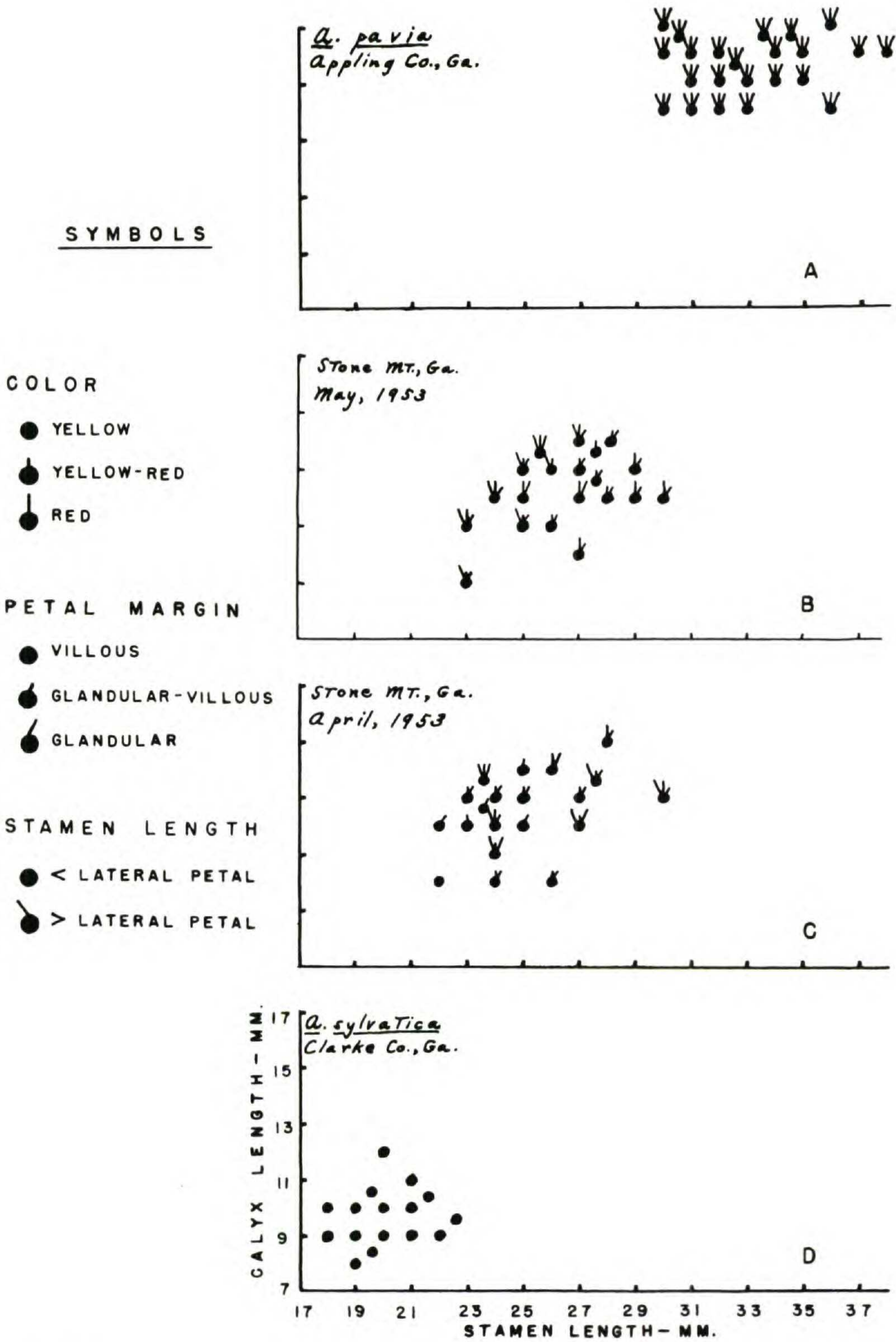


Fig. 1. Pictorialized scatter diagrams of buckeye populations, showing *A. pavia*, *A. sylvatica* and a hybrid swarm at Stone Mountain, Georgia.

are shown in Fig. 1, graphs A and D. It seems obvious from this series of four scatter diagrams that the Stone Mountain population is a hybrid swarm between the suspected *A. pavia* and *A. sylvatica*.

Although every character illustrated has apparently been influenced through hybridization, there is a tendency for the characters of the species to stay together. For example, the red color and the presence of glands on the petal margins are usually closely correlated. With respect to the stamen length vs. calyx length, the entire population is intermediate between the introgressing species. There is, however, relatively little difference between the early- and late-blooming members of the population. If anything, the earlier flowering forms are slightly closer to *A. sylvatica* and more variable. Factors affecting time of flowering appear independent of species differences. Populations of the pure species often show this same variation in time of flowering.

Size and shape of inflorescences seem to be variable in many populations whether hybrid swarms or of pure species. The same variation may even occur on a single shrub (Hardin, 1956). This variation certainly does not seem to be due to hybridization. The variation in pubescence is more or less characteristic of both *A. pavia* and *A. sylvatica*. The variation in this Stone Mountain population is no more extreme than that found in any population of either species. In both species the glabrous form is more often found (at least in eastern populations); however, in nearly every population, slightly tomentose and extremely tomentose leaves are commonly found. These pubescent forms are not recognized by the writer as distinct taxa.

The geographical position of this population is of interest since *A. pavia* is typically found only on the Coastal Plain—some 80–90 miles southeast of Stone Mountain. This hybrid swarm is in the center of the range of *A. sylvatica*. Recent studies of other populations in Georgia and hundreds of herbarium sheets show that *A. pavia*, or at least *A. sylvatica* with a very strong influence of *A. pavia*, extends up the rivers from the Coastal Plain well into the Piedmont. Hybrid populations, for example, are common along the Savannah River far up into northwestern South Carolina. Also the Chattahoochee, Oconee,

Ocmulgee and Yellow Rivers, among others, have served as routes for this apparent gene flow. The population at Stone Mountain is only a few miles west of the Yellow River, so it does not seem too strange to find such a hybrid swarm at this locality in Georgia. It is surprizing, however, that *A. pavia* has had such a very strong influence upon *A. sylvatica* even though it is a considerable distance from the typical range and habitat. Does this indicate that *A. pavia* once was regularly on the Piedmont during times when the Coastal Plain was submerged? There is other evidence from which this may be inferred.

Many such hybrid swarms exist throughout the areas of overlap between species ranges. H. K. Svenson (1941) called attention to one such population in Sequatchie Valley of Tennessee. This population has been seen by the writer and is similar in many ways to the one at Stone Mountain. Introgression is often more the rule than the exception in certain areas. Many populations showing introgression between *A. glabra* and *octandra*, *A. octandra* and *sylvatica*, *A. pavia* and *sylvatica*, and to a lesser extent *A. glabra* and *pavia*, have been found. Certainly not all populations in regions of overlap are hybrid swarms, but rather they often show a heightened variation in the parental species. Analyses of these other populations and a more detailed discussion of introgression within the buckeyes will be reported later.

This Stone Mountain population is a graphic illustration of what has been taking place in many localities within and between species populations of the buckeyes of eastern North America. It is also an illustration of why there has been so much confusion in the taxonomy and field identification of these trees and shrubs. To be sure, within this one population at Stone Mountain there are some shrubs which would be placed without question as *A. sylvatica* (e.g., the types of *A. georgiana* and var. *pubescens*). The disturbing fact, though, to the floristic or herbarium systematists and the field naturalists of the Atlanta area, is that the majority of these shrubs at Stone Mountain cannot be "keyed out" in any floristic manual or guide.

A complete understanding of the buckeyes must include

such intermediate forms and the realization that they are of hybrid origin. Likewise, any usable dichotomous key written for the buckeyes of eastern North America should include these hybrid forms in some way.—DEPARTMENT OF BOTANY, UNIVERSITY OF MICHIGAN.

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NOTES ON THE CLEISTOGAMOUS SPECIES OF POLYGALA IN SOUTHEASTERN UNITED STATES

CHARLES W. JAMES

In Blake's (1924) monograph of the *Polygalaceae*, two cleistogamous-flowered species of *Polygala* were included for the southeastern United States: the wide-ranging *P. polygama* Walt., known from Florida to Texas and as far north as Minnesota, Ontario, Quebec and Nova Scotia, and *P. lewtonii* Small, an endemic of the sand-scrubs of central Florida. Earlier, Blake (1915) described *P. polygama* forma *obovata*, but later (1924) did not consider it, or any other infraspecific taxon of *P. polygama*, worthy of taxonomic recognition. Subsequently, only one other species, *P. aboriginum* Small (1926), has been described. This is a poorly known "species" from the east coast of Florida (Volusia County).

In the present paper, *P. lewtonii* Small is recognized as a valid species. *P. polygama* Walt. forma *obovata* Blake is elevated to the rank of species and is renamed *P. crenata*. *P. aboriginum* Small is regarded as a synonym of *P. polygama* Walt., as is *P. polygama* Walt. var. *obtusata* Chod. The study is based on specimens from the Florida Agricultural Experiment Station Herbarium (FLAS), the Gray Herbarium (GH) and the New York